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Evaluating predation pressure on green treefrog larvae across a habitat gradient

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Abstract The effect of a predator on the abundance of a prey species depends upon the predator's abundance and its ability to capture that prey. The objectives of this research were to evaluate the community structure of predators of green treefrog (*Hyla cinerea*) tadpoles across habitat types and evaluate the effectiveness of individual predators on *H. cinerea* tadpoles. Correspondence and cluster analyses of predator frequencies across 23 aquatic habitats indicated that the majority of variance in predator communities was due to a division between permanent and temporary habitats. Experimental work demonstrated that survival of the smallest *H. cinerea* tadpoles was significantly lower than survival of medium and large tadpoles with the most effective predators, indicating that *H. cinerea* tadpoles attain a refuge from predation at larger body sizes. We combined the effectiveness of predators in experiments with the abundance of each predator species from the predator community survey to demonstrate that predation pressure on *H. cinerea* tadpoles is higher in temporary ponds. This pattern may explain in part why this species generally breeds successfully only in permanent habitats. It also confirms that discussions about an increasing gradient of predation pressure from temporary to permanent aquatic habitats should be restricted to individual prey species for which such a gradient has been demonstrated.

Keywords Community structure · Habitat gradient · *Hyla cinerea* · Predation · Predator–prey interactions

Introduction

The effect of one species on another in communities is a function of the strength of the per capita species interac-

tion and the abundance of each species in the community (Laska and Wootton 1994). An abundant species may have little effect on another species if the per capita strength of interaction is weak; conversely, an uncommon but voracious predator may have a large effect on prey populations (Paine 1974; Schemske and Horvitz 1984). Many studies have demonstrated that single predators have strong effects on prey populations, but in nature most prey are subject to multiple predators (Sih et al. 1998). In order to understand the relative importance of several predator species on a prey species both predator effectiveness and abundance must be considered. However, estimating the importance of predators on a prey species that occurs across a range of habitats is complicated by the fact that the community of predators may vary across habitats.

In lentic freshwater systems, predator community structure varies along a gradient of hydroperiod from ephemeral to temporary to permanent ponds (Wellborn et al. 1996). Ephemeral habitats that fill for only a few weeks or months are generally free of large predators. Temporary habitats that dry every few years are fishless but have invertebrate and caudate larvae predator communities, while permanent aquatic habitats are characterized by large fish predators (McPeck 1990; Werner and McPeck 1994). Most studies of this gradient in hydroperiod focus on the distinction between temporary and permanent habitats, and overall predation pressure is thought to increase across this gradient from temporary to permanent water because dangerous fish predators are found in permanent habitats (Wellborn et al. 1996; Kats et al. 1998).

Prey communities, including assemblages of larval anurans, also vary across this hydroperiod gradient because of differences among species in their capacity to develop quickly in the most ephemeral ponds and their vulnerability to predation in the more permanent ponds and lakes (Morin 1983; McPeck 1990). However, most of the studies that support this generalization have focused on vulnerability of prey to a single, dominant predator species or guild from each habitat type (Werner and McPeck 1994;

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Table 1 Habitat description for localities sampled for analysis of predator community structure

Locality	Habitat type	Census
Airport Pond	Temporary pond	September 2001, May 2002
ANF Pond 1	Temporary pond	September 2001
ANF Pond 5	Temporary pond	September 2001, May 2002, August 2002
ANF Pond 50	Temporary pond	September 2001, May 2002, August 2002
ANF Pond 55	Temporary pond	September 2001
ANF Pond 6	Temporary pond	September 2001, May 2002, August 2002
Hughes Pond	Temporary pond	September 2001, May 2002, August 2002
Fish Pond	Temporary pond	September 2001, May 2002, August 2002
Barn Pond	Temporary pond	September 2001, May 2002
Cool View Pond	Temporary pond	August 2002
Lake Jackson	Thickly vegetated lake	September 2001, August 2002
Little Lake Jackson	Thickly vegetated lake	September 2001, May 2002, August 2002
Lake Iamonia	Thickly vegetated lake	September 2001, August 2002
Moore Lake	Sparsely vegetated lake	May 2002, August 2002
Gannett Pond	Large vegetated pond	September 2001, May 2002, August 2002
Gambo Bayou	Large vegetated pond	September 2001, May 2002, August 2002
Chapman Pond	Small drainage pond	September 2001
Cessna Pond	Sparsely vegetated pond	May 2002
Tram Road	Small vegetated pond	May 2002
Meridian Road	River floodplain swamp	September 2001, May 2002
Rock Bluff	River floodplain swamp	September 2001
MacBride's Slough	Spring creek	May 2002
Gum Pond	Mixed hardwood swamp	September 2001

Van Buskirk and McCollum 1999). While the effects of one predator or type of predator are critical for some species, most of these prey are exposed to many species of predators with different microhabitat occupancy, different foraging modes, different densities, and different per capita consumption rates (Sih et al. 1998).

The examination of how combinations of predators affect a cohort of prey (Travis et al. 1985) has not been extended to studying how a prey species is affected by suites of predators that vary within and among habitat types (Relyea 2002). Consequently, for prey species that are distributed along the hydroperiod gradient, the actual distribution of predation risk and the factors that create differential predation risk are unknown. For example, it might be that the replacement of predator species across the gradient is a replacement of ecological equivalents such that widely distributed species experience little variation in predation pressure (Morin 1995). Alternatively, a species that normally occurs in habitats at one end of the gradient may suffer greater predation risk in habitats at the other end of the gradient because it is not adapted to escape from the types of predators in those habitats (McPeck 1990). Such a pattern would imply that the predation gradient is not absolute but relative to the particular prey species.

In this paper, we address the importance of predation across habitat types and attempt to estimate the intensity of predation pressure for a prey species, the green treefrog (*Hyla cinerea*), that occurs across a range of habitats. First, we present an evaluation of the predator community structure across 23 aquatic habitats. Second, we present

experimental evaluations of the predatory capabilities of ten predators, from the range of habitats, on *H. cinerea* tadpole survival. We combine these two components into an index of relative importance and use this index to evaluate the potential role of predation in the distribution of *H. cinerea* tadpoles.

Materials and methods

Study system

Hyla cinerea occurs throughout southeastern USA from Delaware to Texas and ranges north along the Mississippi River valley into southern Illinois. This species breeds during the summer in a variety of permanent water habitats including lakes, ponds, swamps, and river floodplains (Garton and Brandon 1975; Mount 1975). In addition, *H. cinerea* occasionally breeds in temporary localities (Wright 1932); during this study a few amplexed *H. cinerea* pairs were observed at temporary, fishless ponds. In north Florida we have observed *H. cinerea* breeding choruses from March through September, and tadpoles are present from May through September. *H. cinerea* tadpoles are primarily filter feeders of algae and usually take 30–40 days to metamorphose (Leips et al. 2000). Survival of anuran larvae is highly variable and is strongly influenced by predation (Kats et al. 1988; Morin 1995; Wilbur 1997). Thus, *H. cinerea* is an ideal system to study the variation in predation across habitats because it is a widespread species that breeds in several different habitat types and is probably subject to intense predation pressure during the larval period.

Table 2 Predators used in experiments evaluating tadpole survival.

Tadpole sizes for each stage in parentheses are \bar{x} total length in mm \pm SD. Predator sizes are \bar{x} (SD) in mm of body length for each species. *Dashes* indicate that a predator was not evaluated for that size tadpole

Predator	Scientific name	Predator size for tadpole stage		
		Small (8 \pm 1.5)	Medium (13 \pm 2.4)	Large (27 \pm 3.1)
Aeshnid naiad	<i>Anax junius</i>	30 (5.4)	24 (2.7)	30 (3.3)
Libellulid naiad	<i>Tramea lacerata</i>	19 (2.9)	22 (1.5)	20 (1.3)
Dytiscid larvae	<i>Cybister fimbriolatus</i>	45 (14.1)	43 (12.4)	45 (13.1)
Belostomatid	<i>Belostoma lutarium</i>	21 (3.6)	—	22 (3.7)
Crayfish	<i>Procambarus</i> spp.	63 (14.7)	53 (10.4)	64 (11.7)
Flier sunfish	<i>Centrarchus macropterus</i>	34 (2.1)	35 (1.7)	33 (4.1)
Bass	<i>Micropterus salmoides</i>	34 (3.3)	—	—
Mosquitofish	<i>Gambusia holbrooki</i>	38 (3.1)	—	—
Newt	<i>Notophthalmus viridescens</i>	43 (11.4)	43 (8.9)	44 (10.4)
Musk turtle	<i>Sternotherus odoratus</i>	75 (3.1)	—	74 (2.6)

Predator community structure

We evaluated predator community structure in three sampling periods at a total of 23 localities where *H. cinerea* breeding choruses occurred. These localities span the range of aquatic habitats in which *H. cinerea* breeds in north Florida (Table 1) including lakes, permanent ponds, swamps, and large temporary ponds. No ephemeral ponds (typical hydroperiod <6 months) were included in this survey. Temporary ponds in this survey were large and retained water for several years between drying events. Censuses were performed at 18 localities in September 2001, at 15 localities in May 2002, and at 12 localities in August 2002 (Table 1). This repeated sampling design allowed us to determine if predator community structure varied temporally. Due to variation in hydroperiod and other factors, not all sites could be surveyed in all sampling periods, thus sample sizes of localities varied across sampling periods. Eight of the localities were surveyed in all three censuses, six of the localities were surveyed in two census periods, and the remaining nine sites were surveyed in one of the census periods.

We surveyed each locality by taking four samples with a 0.5-m² aluminum box sampler (box trap). For each sample, the box trap was thrown into the littoral zone (<50 cm deep) and pushed firmly into the substrate. We chose a 0.5-m² box trap because it has been proven effective at sampling both fishes and invertebrates in heavily vegetated aquatic habitats (Chick et al. 1992; Jordan et al. 1997; Turner and Trexler 1997; Leips and Travis 1999). Macrofauna were removed from the box trap using ten sweeps of a D-frame dipnet (1 mm mesh). All contents of the dipnets from the trap were sorted using small aquarium nets. We identified all macrofauna to the lowest taxonomic level possible, recorded frequency of each taxon, and then released all animals back into the aquatic habitat.

In order to establish that four box trap samples per site were sufficient to accurately quantify the community of predators at each site, we selected four sites to sample more intensively. These sites consisted of two temporary ponds and two permanent ponds. We performed 12 trap samples at each of these sites. We found that the first four trap throws captured on average 80% of the total number of predator species used in our community analysis found at each site. Predator species caught for the first time after the first four throws at each site tended to occur at low overall abundance. Predator species caught in the first four throws occurred in 64% of the total throws at each site and had an average density of 5/m². Predators caught for the first time after the first four throws occurred in 22% of the traps at each site and had an average density of 0.5/m². In addition, the more extensive 12 trap sampling did not uncover any additional potential predator species that could prove important in our analysis. Thus we feel confident that four trap throws at each site is sufficient for quantifying the predator community.

Our data analysis sought to determine what predator species were responsible for the majority of the variation in predator community structure, and which habitats had similar predator communities. Data for each sampling period were analyzed separately. Counts of each species were pooled for all four trap throws at each site. Eight

taxa demonstrated in previous studies to prey on tadpoles were selected for analysis of predator community structure. Four types of insects were selected for analysis: aeshnid odonate naiads (*Anax junius*, *Basiaesha* spp., and others), libellulid odonate naiads (*Tramea lacerata*, and others, Werner and McPeck 1994; Travis et al. 1985), belostomatids (*Belostoma lutarium*, Brodie and Formanowicz 1987), and backswimmers (*Notonecta* spp., Cronin and Travis 1986). In addition, we analyzed frequency of crayfish (*Procambarus* spp., Formanowicz and Brodie 1982), fishing spiders (*Dolomedes* spp., Bleckmann and Lotz 1987), and newt larvae (*Notophthalmus viridescens*, Morin 1983). Finally, we grouped several species of fish into one category named “small fish” to represent overall abundance of predatory fish in the littoral zone. This group included mosquitofish (*Gambusia holbrooki*, Woodward 1983), juvenile sunfish (*Lepomis* spp. and *Centrarchus macropterus*, Werner and McPeck 1994) and topminnows (*Fundulus* spp., Garton and Brandon 1975).

We did not group habitats a priori into separate habitat types but, instead, used analyses that would demonstrate the natural divisions in predator community structure. We used correspondence analysis to examine patterns of predator species occurrence across localities (Legendre and Legendre 1998). This method determines which predator species abundances are correlated with each other and identifies which species are primarily responsible for the overall variation in community structure. We then employed cluster analysis to examine which localities were most similar in predator species occurrences by joining localities with the most similar frequencies of the predator species. For the cluster analysis we used average linkage and χ^2 distance, which allows comparison with the results of the correspondence analysis. To determine the influence of fish abundance on the similarity of predator communities, we performed cluster analysis with and without small fish predators included in the analysis for all three census intervals.

Predation rates

We performed a series of experiments to evaluate the per capita predation rates of ten species of predators on *H. cinerea* tadpoles of three different size classes. We selected predators that represented a wide range of foraging modes and habitat occurrences. All animals were maintained and experiments were performed in a large greenhouse facility under natural photoperiod and temperature fluctuations. Limits to the numbers of predators we could collect did not permit all predators to be used for all size classes of tadpoles. For small tadpoles, we were able to study ten predator species, while for medium and large tadpoles we were able to study six and eight predator species, respectively (Table 2). Predators used in all experiments included flier sunfish, dytiscid beetle larvae, crayfish, adult newts, aeshnid odonate naiads and libellulid odonate naiads. Experiments on large and small tadpoles also included belostomatids and musk turtles. For experiments with small tadpoles we also evaluated mosquitofish and juvenile bass (Table 2). Predators were

Table 3 Summary of correspondence analysis of predator community structure across habitats. Abundance of eight predator species were used in this analysis: aeshnid and libellulid odonate naiads,

belostomatid, crayfish, *Dolomedes*, small fish (*Gambusia*, *Fundulus*, and Centrarchids), newt, and notonectid

Census	Percentage of variance per axis			Species contributing to axis (%)		Squared contribution to axis (%)	
	1	2	3	1	2	1	2
September 2001	44	24	16	Small fish (–75) Notonectid (+14)	Crayfish (–64) Notonectid (–16)	Small fish (0.96) Notonectid (0.37) Aeshnid (0.33)	Crayfish (0.78) Newt (0.38) Notonectid (0.22)
May 2002	36	34	16	Crayfish (–58) Libellulid (+34)	Small fish (–47) Crayfish (+22)	Libellulid (0.74) Crayfish (0.70)	Small fish (0.83) Aeshnid (0.45)
August 2002	48	22	17	Small fish (–79) Libellulid (+18)	Belostomatid (–91) Crayfish (+6)	Small fish (0.99) Libellulid (0.87)	Belostomatid (0.95) Crayfish (0.10)

collected by dipnet and seining from various aquatic habitats. Due to limitations in the number of some predator species that could be collected, some predators were reused from one experiment to the next, but the same predator individual was never used more than once in an experiment for the same size tadpole. The newts, belostomatids, dytiscid larvae, and musk turtles were reused in all experiments (only four individuals of each predator were collected). In addition, some flier sunfish, aeshnids, and crayfish were re-used. To control for the possibility of predator learning for individual predators used in more than one experiment, all predator individuals used in all experiments were allowed to feed on *H. cinerea* tadpoles prior to use in experiments. Thus we assumed that all predators had a similar amount of experience capturing and consuming *H. cinerea* tadpoles. For analysis, each observation was considered independent. All predators were kept in the greenhouse and fed *H. cinerea* tadpoles and small fish (*Heterandria formosa*) ad libitum prior to use in experiments. Invertebrate predators were maintained in plastic tubs and vertebrate predators were maintained in individual aquaria with filters when not being used in experiments. Immediately prior to use in an experiment all predators were kept without access to food for 14 h.

Two collections of *H. cinerea* eggs were necessary to provide tadpoles of appropriate sizes for the experiments. Over the two collection intervals we collected 13 amplexed pairs of *H. cinerea* from three permanent habitats (Harriman Pond, Chapman Pond, and Lake Jackson) in Leon Co., Fla., USA. Amplexed pairs were maintained overnight in covered buckets of well water in which eggs were laid, adult frogs were then released at the site of capture. Eggs from all egg clutches were mixed thoroughly and then separated into six large aquaria (76 cm × 32 cm × 47 cm) filled with well water to a depth of 30 cm and aerated with an airstone. After hatching, tadpoles were fed a mixture of ground rabbit chow (Manna Pro Corporation, St. Louis, Miss., USA) and TetraMin fish flakes (Tetra Sales, Blacksburg, Va., USA) ad libitum and partial water changes were performed daily. Tadpoles were maintained under these conditions until they had reached the appropriate size for each experiment.

We performed the predation experiments in 1 m diameter wading pools filled with well water to a depth of 12 cm. Two types of refuge were provided in each pool: a large folded mesh structure to mimic aquatic vegetation, and flat pieces of mesh that covered 50% of the bottom of the pool to mimic leaf litter. Each assay included four replicates of each predator treatment and a control (no predator). For each set-up, we added 20 tadpoles selected haphazardly from the six stock tanks and 4 ml rabbit chow to each pool at 1130 hours on the first day of the experiment. We photographed the tadpoles in two pools for later measurement of body sizes from the images (total length of each tadpole, using SigmaScan software). We assigned predators randomly and added one predator to each pool at 1330 hours, after tadpoles had acclimated for 2 h. For medium and large tadpole experiments, each set-up ended at 0830 hours on the third day of the experiment (43 h elapsed time), while for small tadpoles, which experienced higher predation rates, each set-up ended at 0830 hours the following morning (19 h elapsed time).

Tadpole survival was censused once for each replicate; at the end of each assay we recorded the number of surviving tadpoles and then emptied and rinsed each pool. Surviving tadpoles were not reused in later experiments.

We did not include control treatments in our analysis because tadpole survival in control treatments was virtually 100%, only one tadpole died in a control pool during all three experiments. We calculated predation rate for each predator as (initial number of tadpoles–final number of tadpoles)/number of hours in experiment. We then square-root transformed this predation rate and compared the predation rate for each predator species among tadpole sizes using a one-way analysis of variance. For predators tested with all three tadpole sizes, we made multiple comparisons using Tukey's post-hoc method with Bonferroni correction.

Predation pressure index

In order to describe the overall predation pressure in each locality sampled, we constructed an index by multiplying the predation rate (tadpoles consumed per hour) on small tadpoles for each predator by the density of that predator at each site. We only present data from the results of the September 2001 census because this included the greatest number of habitats and results from the other two censuses were similar. The only predators for which we constructed an index were predators we had tested in experiments. We chose predation rate on small tadpoles because this stage of tadpole was most vulnerable to predation, and we tested the maximum number of predators on this stage tadpole. To construct the index for newts we combined density of newt larvae from the sampling with effectiveness of adult newts in the experiments. For sunfish and aeshnid and libellulid odonate naiads, we pooled the density of all species of these taxa in the census and combined it with experimental data for the one species of each taxa tested in the experiments. Thus our index provides an estimate of the total predation pressure suffered by *H. cinerea* tadpoles at each locality based on the abundance and effectiveness of each predator species present.

Results

Predator community structure

Abundance of predator species varied across the habitats surveyed and over time within habitats that were censused more than once (Fig. 1). The most abundant predator taxa over all habitats were libellulid odonate naiads, small fish, aeshnid odonate naiads, and crayfish (Fig. 1). Correspondence analysis revealed significant covariation in abundances of predator species; for all three censuses the first

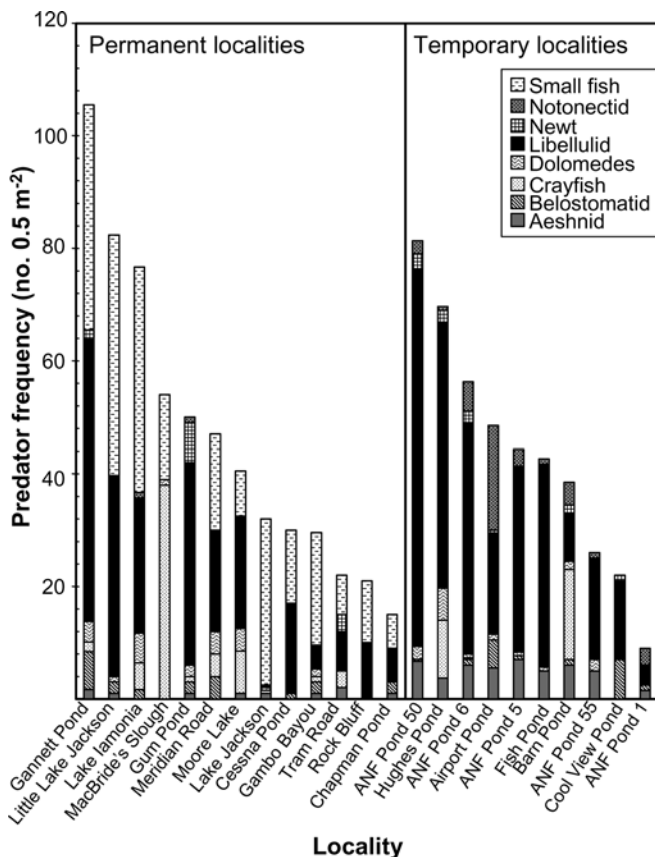


Fig. 1 Abundance of eight predator taxa of green treefrog (*Hyla cinerea*) tadpoles in 23 localities. Censuses are combined for this graph; frequency of predators for localities censused more than once are mean values across all census intervals

three axes accounted for 84–87% of the variance in the data (Table 3). In the September 2001 and August 2002 censuses, the primary axis of variation was determined by negative correlations of fish with notonectid or libellulid abundance, respectively (Table 3). The primary axis for the May 2002 census was determined by negative correlations between crayfish and libellulid abundance (Table 3). Crayfish contributed to the second axis consistently in all censuses, along with notonectid, small fish, and belostomatid abundance (Table 3). Because fish abundance was a factor in the first two axes for all censuses, this analysis indicated that the main division in predator communities is along a permanent (fish abundant) to temporary (fish absent, libellulids and notonectids abundant) gradient. Cluster analysis using the same eight predator taxa as the correspondence analysis supported this division in community structure: in all three censuses the fishless, temporary habitats tended to group together separately from the permanent habitats with fish (Fig. 2). In the May 2002 census, fish were less important in the correspondence analysis, and the permanent habitats grouped less strongly together in the cluster analysis.

Within the permanent habitat group, localities of the same habitat type did not tend to group together (Table 1, Fig. 2). In general, localities censused over more than one census did not consistently group with the same localities

over the three census intervals. After removal of small fish from the analysis, the temporary ponds were grouped less strongly together (Fig. 2d–f), indicating that the invertebrate communities in some permanent habitats may be more similar to communities in temporary habitats. The communities in the temporary ponds diverged over time. In the September 2001 census, the distances between the temporary habitats are relatively small (Fig. 2a). However, in the May 2002 and August 2002 censuses, the distances are larger and some temporary ponds are grouped most closely with permanent localities, even when fish are included in the analysis (Fig. 2b,c).

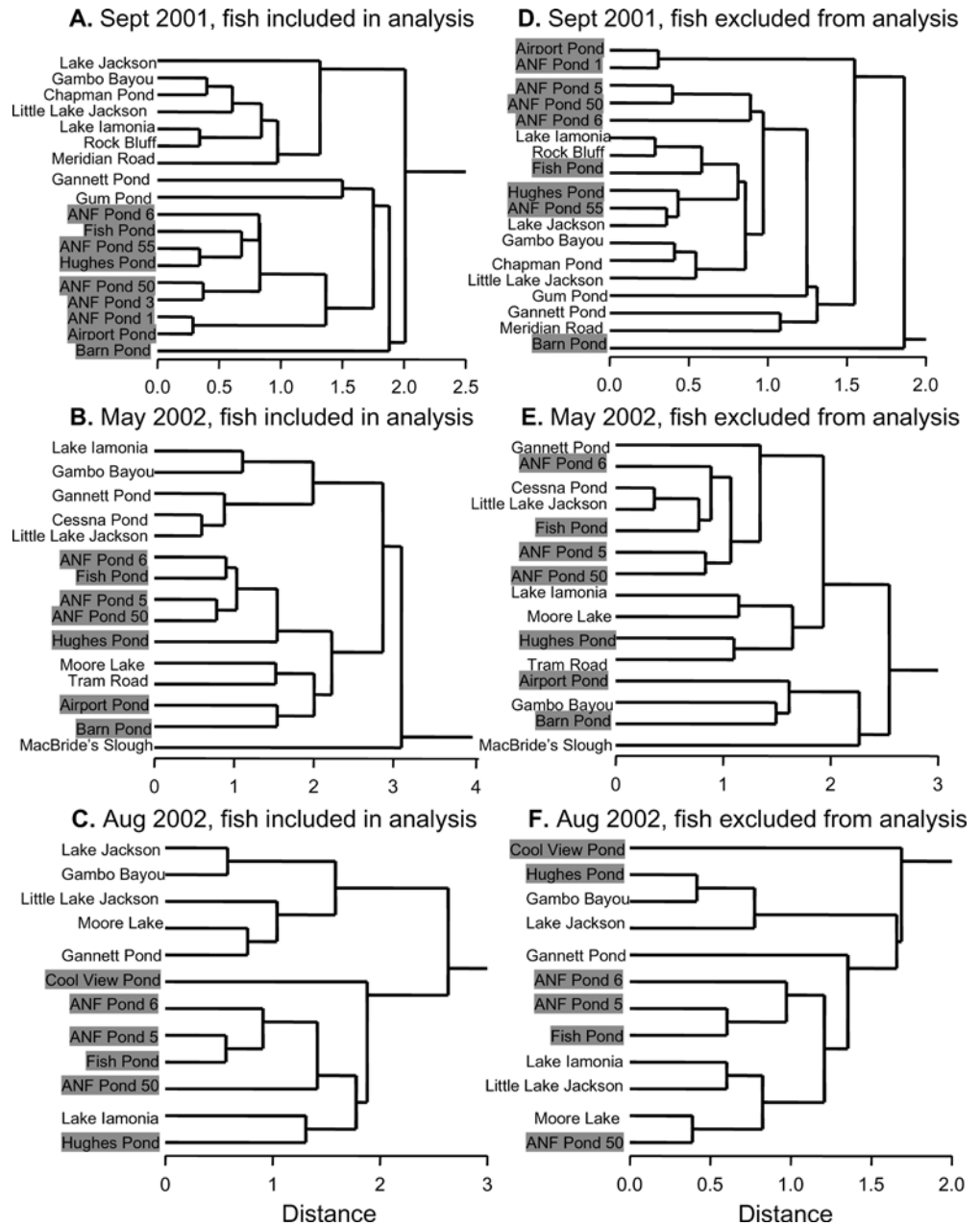
Predation rates

Hyla cinerea tadpoles were susceptible to all of the predators used in these experiments, but predation rates varied widely among predators and across tadpole size classes (Fig. 3). The most effective predators were bass, newts, and aeshnid and libellulid odonate naiads. In general, predation rates decreased with increases in tadpole size for all predators but the rates of predation and the pattern of the decrease with increasing tadpole size differed among predators (Fig. 3). Predation rates for large tadpoles were generally negligible, which indicates that *H. cinerea* tadpoles achieve a size refuge from overall predation long before metamorphosis. However, the size at which tadpoles achieved this refuge varied across predator species. While aeshnids and belostomatids consumed small tadpoles at a high rate, they were less effective at consuming medium and large tadpoles. In contrast, newts, libellulids, and crayfish remained effective predators on medium tadpoles; the estimated predation rate on medium tadpoles was below that for small tadpoles for all three predators but these rates were not significantly different by the multiple comparison criterion for newts and crayfish. Predators that did not have significantly different predation rates across tadpole sizes were dytiscid larvae, flier sunfish, and musk turtles. In general, predators with low predation rates tended to have less variation in predation rate across tadpole sizes while predators with high predation rates exhibited decreasing predation rate with increasing tadpole size.

Predation pressure index

The total predation pressure index, calculated from predation rates on small tadpoles and predator abundance in the September 2001 census, varied across habitats from a high of over 54 at Gannett Pond to a low of less than nine at Lake Jackson (Fig. 4). The importance of individual predator species varied across habitats, implying that there is no single dominant predator for this species at either end of the hydroperiod gradient. Libellulids were the most important predators at every locality except Lake Jackson. Aeshnids were the second most important predator in ten of the localities. Other

Fig. 2a–f Cluster analysis of localities grouped based on similarity of frequency of predator taxa. Censuses for September 2001 (**a, d**), May 2002 (**b, e**), and August 2002 (**c, f**) were analyzed separately. Each analysis was performed including small fish frequency (eight predator taxa, **a, b, c**) and without small fish (seven predator taxa, **d, e, f**). Temporary pond locality names are shaded (for habitat descriptions see Table 1). Note x-axis (distance) scale varies for each graph



predators that contributed strongly to the total predation pressure index in some habitats were belostomatids, crayfish, newts, and mosquitofish. Dytiscid larvae and sunfish were contributors to total predation pressure in four localities. Because no musk turtles or bass were captured in the box trap at any localities during the field sampling, these predators had an importance value of zero in each habitat. In general, temporary habitats had higher overall predation pressure values ($\bar{x} = 28$ tadpoles consumed/h/m²) than permanent habitats ($\bar{x} = 21$ tadpoles consumed/h/m²), a striking result in light of the fact that *H. cinerea* breeds predominantly in permanent habitats.

Discussion

The main division in predator community structure was between temporary and permanent habitats, similar to other studies of freshwater habitats (Wellborn et al. 1996). The presence of fish in permanent habitats is usually assumed to be the factor that influences which prey species occur in these habitats (Kats et al. 1988). While our correspondence analysis indicates that the primary division among habitats is the variation in fish abundance, variation in the abundance of specific invertebrate predators also contributed strongly to the divisions among predator communities.

The individual fish species examined in this study varied in their importance due to variation in abundance and effectiveness. Although bass were very effective

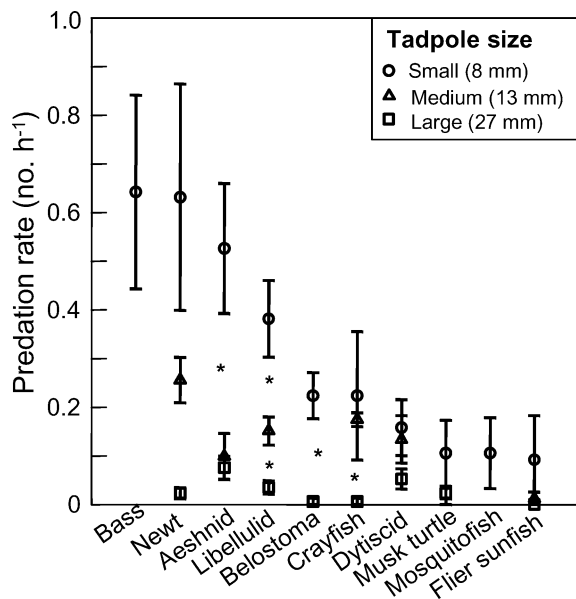


Fig. 3 Predation rate (initial number of tadpoles–final number of tadpoles)/number of hours in experiment) on three sizes of *H. cinerea* tadpoles (ten, six, and eight predator species analyzed for small, medium, and large tadpoles, respectively). Means are \pm SE. An asterisk is placed between means for each predator type that are significantly different (ANOVA $P < 0.05$ with Tukey's post-hoc means comparisons and Bonferroni corrections for predators tested on all three sizes of tadpoles). For newts means for large and small tadpoles differed but neither of these was significantly different than medium tadpoles

predators, they did not appear in our censuses; in contrast, mosquitofish, though weak per capita predators, were abundant at most permanent habitats. This could be due to behavioral differences in these species and habitat use; bass are fast swimmers and probably forage widely through a large area of open water (Heidinger 1975). In addition, juvenile bass of the size used in our experiments are typically found in deeper (0.5–1.5 m) water than green treefrog tadpoles (<0.5 m) (M. Aresco, personal communication, M. Gunzburger, unpublished data). In the experiments, bass were the most effective predator overall, while flier sunfish and mosquitofish were the two least effective predators. Although large-sized predatory fish may exert considerable predation pressure on *H. cinerea* tadpoles (Blouin 1990), we did not use these predators in our experiments because we feel that their extremely low abundance in the censuses indicates that they are not consistently present in the same habitat as tadpoles.

Our cluster analysis divided the predator communities between permanent and temporary localities, but these habitats did not separate completely in the predation pressure index. Six of the eight localities with the highest predation pressure index were temporary ponds, but the habitat with the highest overall predation pressure was a permanent pond (Fig. 4). Our study demonstrates that *H. cinerea* is exposed to highly variable predation pressure across habitats in which it breeds. The most abundant and important predator in most habitat types was libellulid odonate naiads, however there was much variation in the

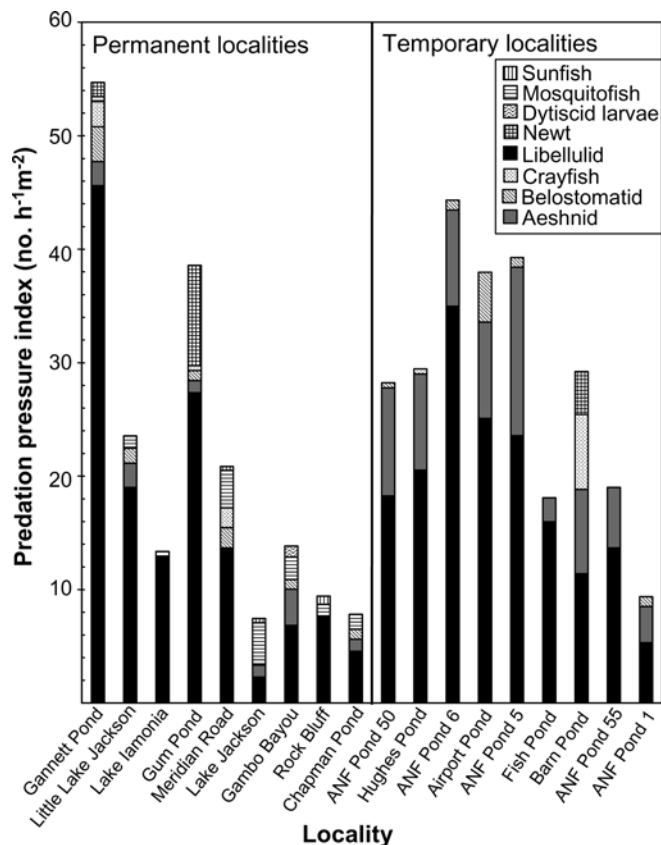


Fig. 4 Predation pressure index (number of small tadpoles consumed/hour \times density of predator at each site) for each locality. Height of bar is total predation pressure index for that locality. Data are from September 2001 census only

importance of this predator type across habitats (Fig. 4). The highest importance index value for libellulids was more than ten times higher than their lowest importance index value (Fig. 4). The variation in predator community structure across habitats and over time, and the potentially high amount of adult dispersal, would both be expected to contribute to generalized antipredator defenses in *H. cinerea* tadpoles and not the evolution of specific adaptations to particular predators (McPeck 1997).

Hyla cinerea breeds predominately in permanent aquatic habitats, but we observed a few *H. cinerea* calling males, amplexed pairs, tadpoles and metamorphs at several temporary ponds (M. Gunzburger, unpublished data). Our predation pressure index suggests *H. cinerea* tadpoles may not usually be found in temporary ponds because predation pressure for this species is greater in temporary ponds than in permanent ponds. However, because predator community structure is heterogeneous across habitats and *H. cinerea* tadpoles reach size refuges from different predators at different sizes, the dynamics of *H. cinerea* populations probably vary considerably across localities in which it breeds. Adult *H. cinerea* may have a mechanism to evaluate the predator community structure of potential breeding sites and thus usually avoid ovipositing in temporary ponds (Resetarits and Wilbur 1991).

Our predation pressure index is an admittedly simple metric. The index takes the predation rates from our experiments as a constant, whereas the rate at which a single predator attacks and consumes *H. cinerea* tadpoles could vary across habitats due to abiotic characteristics, interactions with other predators, the availability of alternative prey, or the effects of the functional response of each predator to prey density, none of which inform our index. Our experimental numbers probably represent the higher part of the range of overall consumption rates, which would make our index too high in its absolute value. We do not expect the index to be biased in different directions for the different predators or the different locations, which would obviate our conclusions. We know that many of these predators engage in intraguild predation if there is an adequate size difference among individuals (M. Gunzburger, unpublished data) and these predators prey on species other than *H. cinerea* tadpoles; however there is no reason to believe that this effect unfolds in a pronouncedly different fashion in different habitats. As a comparative metric, our index provides a useful estimate of the predation pressure across habitats and allows a better understanding of the components of that pressure.

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